

DISTRIBUTION AND DENSITY OF PREJUVENILE Penaeus SHRIMP
IN GALVESTON ENTRANCE AND THE NEARBY GULF OF MEXICO (TEXAS)

by

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Abstract

In early 1959 the Bureau of Commercial Fisheries began a study to determine when, from what direction, at what stage of development, under what conditions, and in what quantity prejuvenile shrimp of the commercially important Penaeus enter the extensive Galveston (Texas) estuary. The findings were to aid in circumscribing offshore spawning areas and thereby provide information on the degree to which the progeny of shrimp reproducing in each area are nurtured in specific estuaries bordering the northern Gulf of Mexico.

Analysis of over 3,000 samples collected systematically during one biological year revealed: That the frequency of sampling, although high, was insufficient to trace the rapid onshore movement of recently hatched broods of Penaeus; that the gross horizontal distribution of Penaeus larvae and postlarvae in the Gulf and vertical distribution of postlarvae in Galveston Entrance changed markedly from season to season; that Penaeus larvae, rarely occurring within 10 km of shore, were not bottom-dwellers; and that Penaeus postlarvae did not frequent the bottom in winter and otherwise were usually more abundant at mid-depths than at the bottom. For estimating density of prejuvenile penaeids, the study's sampling scheme was relatively efficient in controlling spatial variation but comparatively inefficient in accounting for wide temporal variation in organism abundance.

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REPARTITION ET DENSITE DES STADES PREJUVENILES DE CREVETTES Penaeus DANS LA
BAIE DE GALVESTON (TEXAS) ET LES SECTEURS AVOISINANTS DU GOLFE DU MEXIQUE

Résumé

Au début de 1959, le service des pêches commerciales des Etats-Unis d'Amérique a entrepris une étude visant à déterminer à quelle date, de quelle direction, à quel stade de développement, dans quelles conditions et en quelles quantités les stades préjuvéniles de Penaeus, crevettes d'importance commerciale, pénètrent dans la vaste baie de Galveston (Texas). Ses conclusions devaient aider à circonscrire les aires de reproduction du large, et à obtenir ainsi des renseignements sur la mesure dans laquelle les descendants des crevettes ayant "frayé" dans chacune de ces aires se développent dans les diverses baies de la partie septentrionale du golfe du Mexique.

L'analyse de plus de 3,000 échantillons recueillis systématiquement pendant une année biologique a révélé les faits suivants : la fréquence de l'échantillonnage, bien qu'élevée, n'a pas permis de suivre le déplacement rapide des Penaeus récemment écloses vers le rivage; la répartition horizontale approximative des larves et postlarves de Penaeus dans le golfe du Mexique et la répartition verticale de postlarves dans la baie de Galveston accusent de nettes modifications saisonnières; les larves de Penaeus, rares à moins de 10 km du rivage, ne sont pas benthiques; enfin les postlarves de Penaeus ne fréquentent pas le fond en hiver et sont par ailleurs plus abondantes à profondeur moyenne que sur le fond. En ce qui concerne l'estimation de la densité des Penaeidae préjuvéniles, le mode d'échantillonnage utilisé pour l'étude est relativement bon pour mesurer les variations spatiales de l'abondance des organismes, mais comparativement inefficace pour rendre compte des fortes variations temporelles.

DISTRIBUCION Y DENSIDAD DEL CAMARON PREJUVENIL Penaeus
EN LA EMBOCADURA DE GALVESTON Y EN EL CERCANO
GOLFO DE MEXICO (TEXAS)

Extracto

A principios de 1959 la Oficina de Pesca Comercial inició un estudio para determinar el período en que penetran en el amplio estuario de Galveston (Texas) las formas juveniles de las especies Penaeus de camarón de importancia comercial, la dirección de que proceden, la fase de desarrollo en que se encuentran, las condiciones en que están y su cantidad. Los resultados ayudarán a circunscribir las zonas de desove frente a la costa, proporcionando información sobre la medida en que la progenie del camarón que se reproduce en cada una de las zonas, se alimenta en los estuarios que bordean la parte septentrional del Golfo de México.

El análisis de más de 3.000 muestras reunidas sistemáticamente durante un año biológico revelaron que: aunque el muestreo se hacia con frecuencia, no bastaba para determinar el rápido movimiento hacia la costa de las larvas de Penaeus después de la eclosión; que la distribución horizontal aproximada de las larvas y postlarvas de Penaeus en el Golfo y la distribución vertical de las larvas en la entrada de Galveston cambiaban mucho de una temporada para otra; que las larvas de Penaeus, que raramente existen a menos de 10 km de la costa, no habitaban en el fondo, y que las postlarvas de Penaeus no frecuentaban el fondo en invierno, abundando más en general a profundidades medias que en el fondo. En la estimación de la densidad de peneidos juveniles, el plan de muestreo del estudio era suficiente para controlar la variación espacial, pero insuficiente para explicar la amplia variación temporal de abundancia de organismos.

1 INTRODUCTION

For nearly as long as Gulf of Mexico shrimp resources have yielded what is now our most popular seafood, fishery biologists have sought to delineate the oceanic spawning grounds of the three major species, namely, the brown (Penaeus aztecus Ives), white (P. setiferus Linnaeus), and pink (P. duorarum Burkenroad) shrimps. From numerous observations we may safely infer that each species passes through a similar life cycle, which entails spawning and hatching in the littoral zone of the Gulf, mass shoreward movement of the metamorphosing larvae, rapid growth of the young shrimp through post-larval and juvenile stages in estuarine nursery areas, and, within a year, their return as subadults to the sea where the life cycle is completed (e.g., Weymouth, Lindner and Anderson, 1933; Burkenroad, 1934; and Pearson, 1939). Centers of spawning for the three species have not been precisely circumscribed, and, as a consequence, the spatial relation of these centers to specific inshore nursery areas remains to be established.

In the late fifties the Bureau of Commercial Fisheries Biological Laboratory in Galveston, Texas, undertook a series of projects aimed at broadening our knowledge of the shrimps' early life history. The first of these - the subject of this report - was initiated in early 1959 to determine when, from what direction, under what conditions, at what stage of development, and in what quantity recently hatched shrimps of the genus Penaeus enter Galveston Bay, one of the more important nursery areas along the Gulf coast.

2 THE SAMPLING SCHEME

2.1 The study area

Galveston Entrance together with Bolivar Roads, a major artery for waterborne commerce and one of two areal subdivisions established at the study's outset, is the largest of three tidal passes connecting the Galveston Bay complex with the Gulf of Mexico. Shoaling in the Entrance is controlled by two jetties, the distance between which averages just under 3 km (Fig. 1). Mean depth, excluding the area occupied by ship channels, is approximately 4 m; the ship channels themselves are maintained at about 11 m. Surface area (within the inset of Fig. 1) amounts to almost 35 km². Maximum predicted tide differential is roughly 0.5 m and volumetric exchange between the bay and ocean is considerable. The other two tidal inlets are San Luis Pass 48 km to the west and Rollover Pass 32 km to the east. In cross-sectional area both are small relative to Galveston Entrance-Bolivar Roads.

The principal subdivision of the study area included slightly over 1,500 km² of the Gulf lying in a semicircle with focal point at Buoy No. 2 just outside the Entrance jetties (Fig. 1). Depths within this subdivision ranged from 0 to 18 m, the average being about 14 m. Bottom topography is unsculptured, of very shallow gradient, and virtually free of natural impediments.

2.2 Intensity of sampling

To provide a network of "offshore" sampling stations from which counts of larvae and postlarvae would indicate routes of penaeid movement into Galveston Bay, we established four 30-km transects radiating seaward from Buoy No. 2 (Fig. 1). Numbered from I to IV, each transect bisected and identified areal sectors of roughly equal size. Positioned along each transect at intervals from the focus of 1/2, 9, 17 and 24 km were four sampling stations. Thus, four tiers of four stations equidistant from the focus identified parcels of water situated at increasing distances from the Entrance. At each station, samples were collected simultaneously at each of two depths, 1 1/2 and 6 m, and occasionally on the bottom, so that every sampling day yielded not less than 32 collections. (The study began with twice the number of radiating transects and corresponding sampling stations, but was reduced by one-half following the second excursion. In the subsequent analyses, data from the first 2 sampling days were consolidated to conform to the modified scheme described above.)

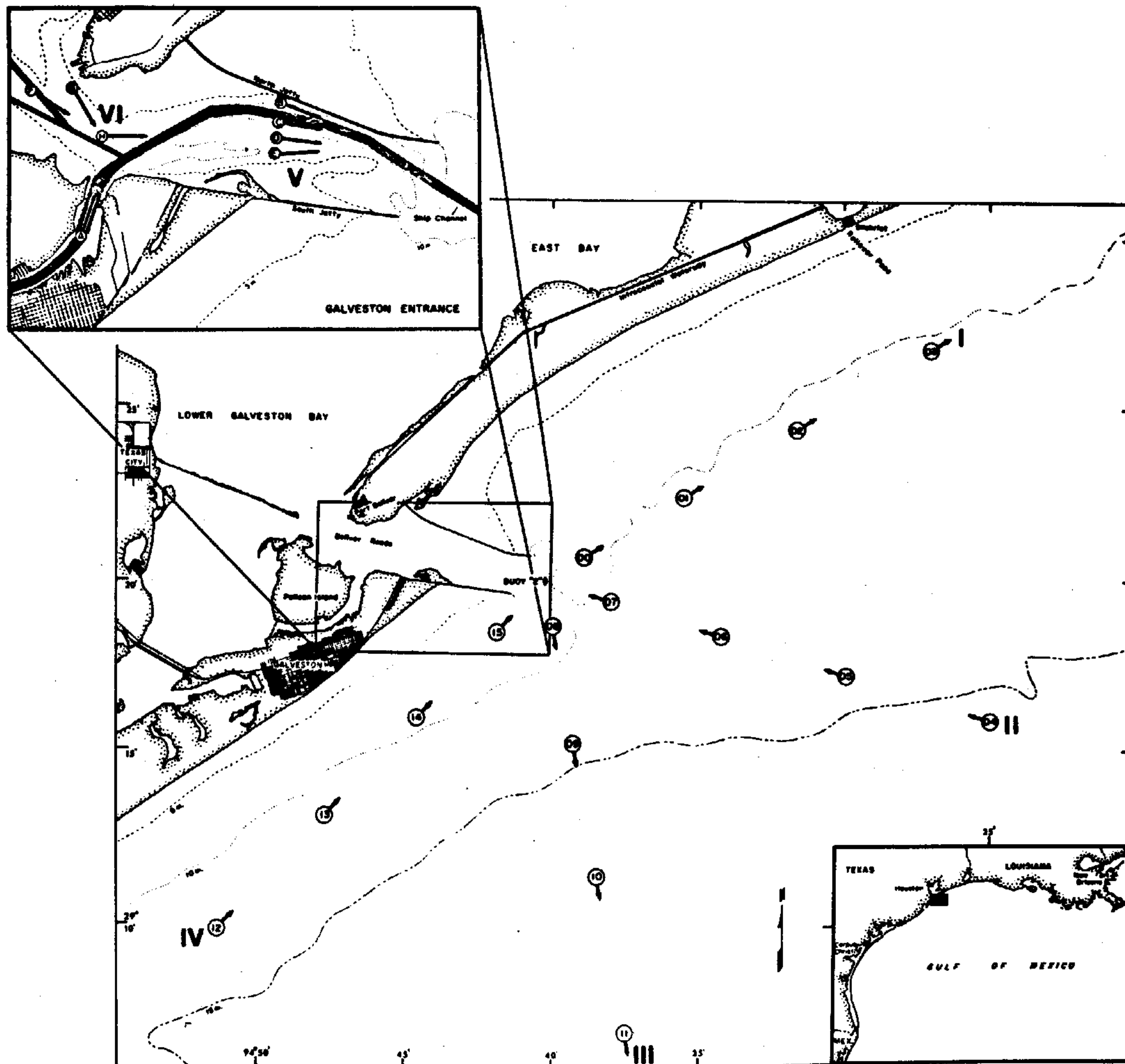


Fig. 1 Chart of Galveston Entrance and the nearby Gulf of Mexico, showing sampling scheme employed in each of these two subdivisions of the study area.

The Galveston Entrance-Bolivar Roads, or "inshore", subdivision of the general study area was further divided into outer and inner sections, identified in Fig. 1 by Roman numerals V and VI, respectively. In each section we established four sampling stations using navigation buoys and other fixed structures as positioning aids. Samples were taken simultaneously at two depths, 1½ and 6 m, and infrequently at the bottom. Each sampling operation resulted in 16 or more collections until one-fourth of the study had elapsed, after which the number was reduced to 12 with the elimination of two stations in section V.

2.3 Frequency of sampling

Beginning 17 March 1959, and ending 21 March 1960, the study lasted 53 wk - one biological year. The offshore stations were occupied once every 9 days for a total of 40 sampling days and 1,410 collections, the inshore stations once every 3 days for a total of 113 days and 1,594 collections (Table I)^{1/}. Sampling offshore required 10 to 12 h depending on sea conditions, whereas sampling inshore took 2 to 3 h. To counter possible bias arising from diel differences in the vertical distribution of planktonic *Penaes*, we routinely sampled (with one exception) during daylight. For a comparable reason most (nearly three-fourths) inshore samples were collected on flood tides or adjacent low and high stands.

2.4 Sampling gear

Two double-rigged, Florida-type shrimp trawlers, 14 to 15 m long, provided adequate platforms for all sampling. Sampling gear in a typical operation consisted of a pair of high-speed plankton nets, one fished from each of the two vessel outriggers at each of the two sampling depths, and a small otter trawl towed from a davit for sampling at the bottom.

2.4.1 Description The plankton nets were of the Gulf-V design (U.S. Fish and Wildlife Service, 1959) 40 cm (16 in) in diameter at the mouth, fitted with Atlas flow meters, and constructed of monel cloth having 31.5 meshes per cm (80 meshes/in) and 36 percent open area (Fig. 2). Each net had an absolute open area at the filtering surface 1.67 times the mouth area. Mesh width of 190 µ was sufficiently small to retain the smallest larva we expected to encounter.

The trawl, or "try net", measured 3 m along the headrope, was constructed of 1½-cm (½-in bar) webbing, and had a half-meter No.1 Nansen net fitted over its codend. Its effective mouth opening was slightly less than 2,100 cm².

2.4.2 Calibration Before sampling began and at infrequent intervals during the study, we calibrated each of the four flow meters used interchangeably in our several Gulf-V nets. The uncontrollable effects of differential clogging during calibration trials were obviated by simply calibrating the meters outside the nets. This entailed mounting the four meters on a rigid bar and towing the assembly over known distances within the speed range 1.4 to 1.8 m/sec (2¾ - 3½ k). Vessel speed, hence distance, was logged by measuring with a stop watch the amount of time it took the vessel and a trailing buoy with combined length of exactly 30 m to pass a spot of fluorescein dropped on the sea surface from the bow of the vessel. Each trial run yielded a hypothetical estimate

^{1/} In a few instances individual collections were lost due to gear malfunction or other causes. And, where sampling on rare occasions had to be abandoned because of equipment failure or bad weather, whatever material was collected has been excluded from the following analyses. Every attempt was made to facilitate statistical treatment by minimizing difficulties attributable to missing data.

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TABLE I

Distribution by subdivision, depth, and month of plankton samples collected in the vicinity of Galveston, Texas, March 1959 - March 1960

Subdivision	Galveston Entrance (6-8 stations)					Gulf of Mexico (16 stations)				
Month	Sampling days	Depth			Sampling days	Depth				
		1½ m	6 m	Bottom		1½ m	6 m	Bottom		
1959	<u>Number</u>	<u>Number</u>			<u>Number</u>	<u>Number</u>				
March	6	48	46	0	1	8	8	0		
April	10	72	80	0	3	48	48	9		
May	13	80	104	49	3	48	48	16		
June	12	96	96	5	3	48	48	0		
July	8	42	48	0	4	64	64	0		
August	9	54	54	11	3	48	48	16		
September	8	48	48	7	5	80	80	26		
October	9	54	54	8	3	48	48	18		
November	7	42	42	7	3	48	48	17		
December	10	60	60	10	4	64	64	23		
1960										
January	7	42	42	7	2	32	32	12		
February	8	46	46	8	3	48	48	17		
March	6	36	36	6	3	38	38	12		
Subtotal	113	720	756	118	40	622	622	166		
Total	113	1,594			40	1,410				
Frequency	Every 3 days				Every 9 days					

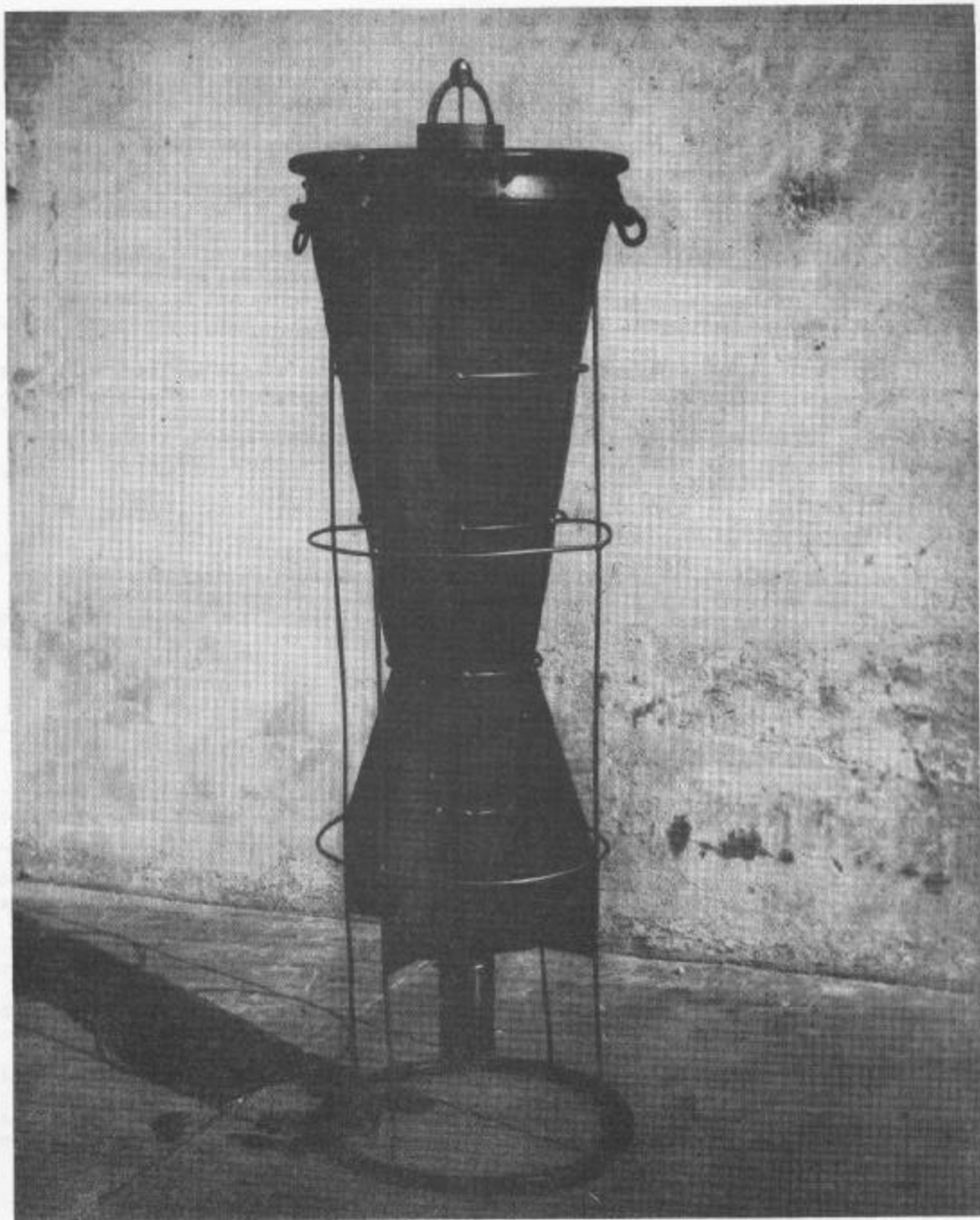


Fig. 2 The high-speed, all-metal, Gulf-V plankton net.

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of filtered water volume (distance \times cross-sectional area of net mouth) and a corresponding meter reading. The resulting coefficients of the regression of volume on number of meter revolutions were used to standardize for quantitative analysis all subsequent plankton counts. Fig. 3 depicts the plot of a typical set of calibration data. Under normal sampling conditions we assumed that the mouth of the net maintained a perpendicular attitude relative to the direction of haul, that added resistance due to clogging during a haul did not significantly alter rate of vessel headway (i.e., net speed), and that the flow meters accordingly registered only the amounts of water actually passing - at a diminishing rate during each haul - through their respective nets. (See Buchanan-Wollaston (1911) for additional observations on the subject of clogging and net performance).

The volume of water filtered during each haul of the trawl was estimated by the product of the effective cross-sectional area of the net's mouth and the distance of the haul, as measured by the method just described.

2.4.3 Operation Net hauls lasted 10 min and, as stated earlier, were made at 1½ m, 6 m and, infrequently, on the bottom. They originated at and proceeded in the direction from the sampling stations indicated in Fig. 1. Maintaining the Gulf-V nets at their designated sampling depths presented no problem; quick, vertical entry and retrieval of the nets with the vessel stopped at the beginning and end of every haul precluded significant contamination of the samples.

2.5 Measurement of environmental factors

By means of remote-sensing devices, vessel personnel continuously recorded water temperature and salinity at 3 m during operations at selected stations throughout the study area. Whenever recording instruments became inoperable, the desired measurements were obtained by conventional methods.

3 REDUCTION OF SAMPLE MATERIAL

3.1 Treatment of collections

At the completion of a set of simultaneous hauls, members of the vessel's crew secured the nets in a vertical position and carefully washed the sample material into the respective collecting "cups". From here each collection went into a liter jar containing sufficient buffered formalin to produce a 5-percent preserving solution. After a period of settling at the laboratory, the supernatant preservative was discarded and the sample concentrate transferred to a 250-ml bottle; enough preservative was then readded to fill the bottle.

Laboratory aids trained in identification and subsampling procedures sorted all penaeid-like organisms from the numerous plankton samples. Subsampling entailed the examination and sorting of one or two 50-ml aliquots under a binocular microscope whenever an entire sample could not be scanned efficiently because of too dense a concentrate. Occasionally, when individual aliquots could not be processed for the same reason, the entire 250-ml concentrates were diluted to twice (rarely three times) their original volumes. Subsequent statistical tests showed that subsampling variation, regardless of concentrate dilution, was negligible. All penaeid-like organisms from a sample concentrate or an aliquot thereof were stored in a vial for later identification and enumeration.

3.2 Identification and enumeration of Penaeids

A serious problem in the final stages of sample reduction confronted us during the early part of the study. At that time, there existed little information that aided in the identification of larval and postlarval Penaeidae, represented locally by 5 genera and 12 or so species, all of which on cursory examination appear exactly alike at

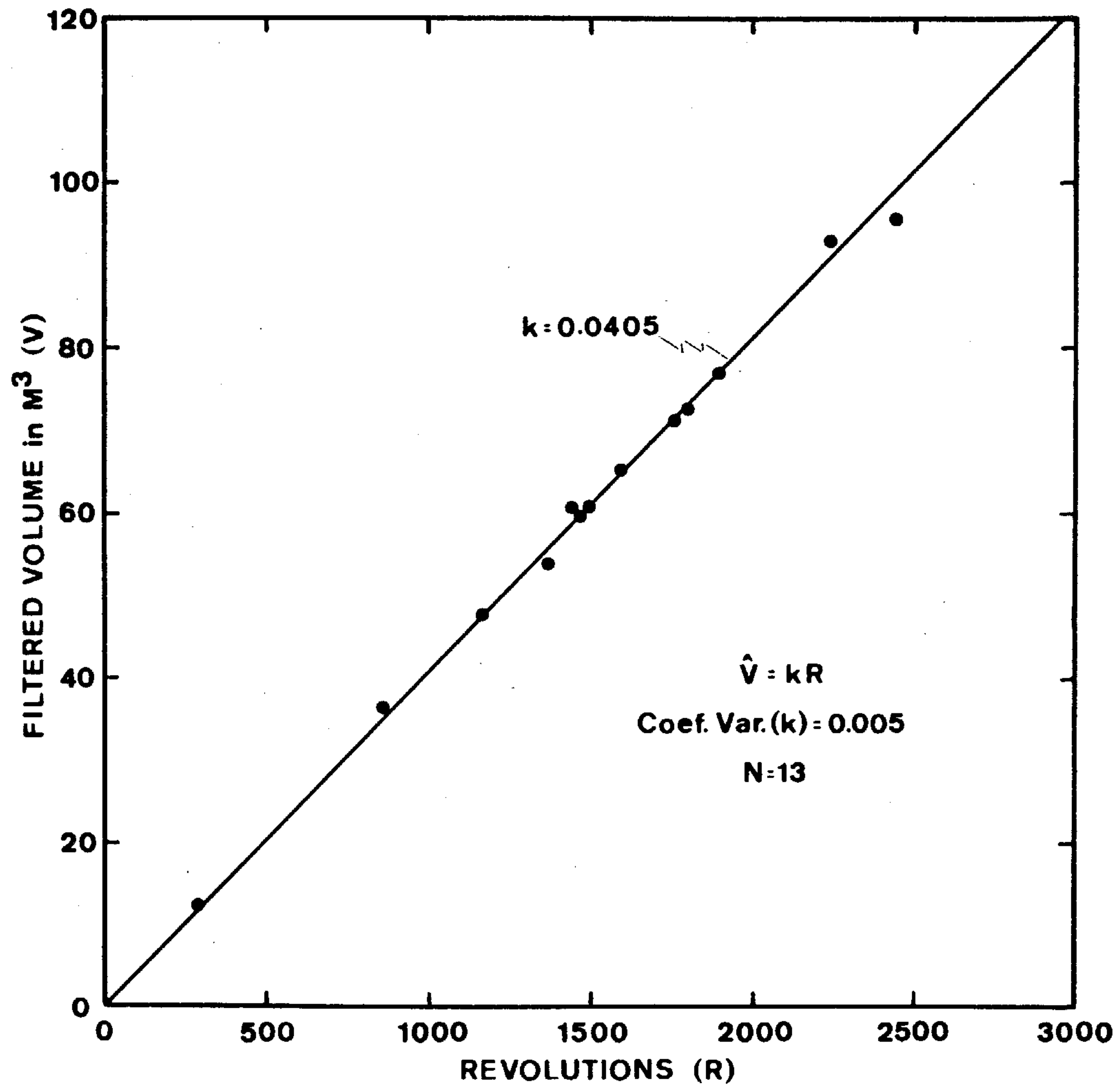


Fig. 3 Typical plot of calibration data for flowmeter used in Gulf-V plankton nets.

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corresponding stages of early development. Consequently we had to employ coding systems by which to classify sample components until positive identification could be made. Since 1960, however, a considerable amount of comparative study has resulted in descriptions and keys which facilitate identifying to genus and, in some cases to species, littoral penaeids collected from the Gulf as protozoae, mysids, and postlarvae (Dobkin, 1961; Renfro and Cook, 1963; Cook, 1966; and Cook and Murphy, 1965). Positive identification of eggs and nauplii is still not practicable.

To the extent that this information permitted, we satisfactorily identified the sampled penaeids with one notable exception: It was not possible to separate larval and early postlarval brown and white shrimp, the predominant and commercially most valuable species in the northwestern Gulf.^{2/} We therefore combined them under the heading Penaeus and, as necessary in interpreting the data, distinguished between them on the basis of their expected seasonal distributions. In addition, the collections yielded members of three other genera - Sicyonia, Trachypenaeus, and Xiphopenaeus - but, except when evaluating the sampling scheme, all subsequent discussion deals solely with Penaeus.

After sorting to genus (or species) and stage of development, subsample elements were counted and the resulting totals adjusted to numbers per 100 m³ by the calibration factors described earlier.

4 DISTRIBUTION OF PREJUVENILE Penaeus

We had hoped at the study's outset to sample at the offshore stations with sufficient frequency to trace the day-to-day movement of broods of young shrimp toward and into Galveston Entrance, but quickly found it impractical to do so because of manpower limitations. Instead of sampling in the Gulf once every 3 days as originally scheduled, we restricted our runs to once every 9 days, and thereby had to forgo information on rate of inshore movement. We did obtain some indication of the seasonal distribution of larval and postlarval Penaeus by area, depth, and stage of development, however, and also made a few observations on the diel distribution of postlarvae in Galveston Entrance.

4.1 Distribution by area and depth

Although the study's sampling coverage in space and time might be considered impressive by ordinary standards (Table I), the lack of positive results materially hampered statistical analysis. The results we did obtain confirmed what many others have observed, namely, that Penaeus shrimp larvae and postlarvae, while at times very abundant, are nevertheless rather elusive organisms with a distinct tendency to aggregate. That contagion is perhaps the most notable characteristic of their population distributions is attested by the data in Table II. As a consequence, the standardized counts (or their means) have been treated in the following analysis as Poisson variates and transformed accordingly by the function

$$\sqrt{x + 3/8}$$

as suggested by Rao (1952). Analysis was facilitated further by grouping the data by seasons (spring - March, April and May; summer - June through August; etc.).

To test for differences between mean sample counts from different levels of the same source of variation, we employed with the data from our offshore sampling an analysis of variance of transformed counts arranged in a 4x4x2 factorial design;

^{2/} Some larvae and postlarvae of pink shrimp, the other local Penaeus, may have been included but this likelihood is considered small because adults and juveniles are infrequently observed in the Galveston area.

TABLE II

Distribution of prejuvenile Pennaeus among
2,720 plankton samples collected with Gulf-V
nets in the vicinity of Galveston, Texas,
March 1959 - March 1960

Organisms per 100 m ³ per sample	Subdivision		
	Galveston Entrance	Gulf of Mexico	Combined
<u>Number</u>		<u>Number</u>	
0- 9	1,282	1,163	2,445
10- 19	68	44	112
20- 29	37	17	54
30- 39	23	4	27
40- 49	19	2	21
50- 59	13	4	17
60- 69	2	2	4
70- 79	5	1	6
80- 89	7	1	8
90- 99	2	0	2
100-109	1	1	2
110-119	2	0	2
120-129	2	0	2
130-139	0	0	0
140-149	2	0	2
≥150	11	5	16
Total	1,476	1,244	2,720
Zero entries	1,129	1,020	2,149

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i.e., with sample counts obtained throughout 4 mo, from four areal sectors, at four distances from the survey's focus, and at two depths. Seasonal effects were assumed to be fixed. Difficulties in computation arising from unequal subclass size, caused by failure to collect a small number of samples during bad weather in March 1959 and March 1960, were precluded by adjusting the affected counts to the base subclass size of 10 samples and reducing the error degrees of freedom accordingly.

The resulting analysis suggested that, on the average, the distribution of pre-juvenile Penaeus approaching Galveston Entrance was nearly homogeneous (Table III). Most noteworthy biologically was the significant seasons X sectors interaction, which indicated marked variation in mean numbers of prejuvenile Penaeus among areal sectors within each season. This seasonal change in horizontal distribution is shown graphically in Fig. 4, where it is suggested that in the spring most larvae and postlarvae approached the Entrance from the east, whereas in the summer the preponderance approached from the south and west. There is little doubt in our minds that in the former case the species in question was predominantly brown shrimp, in the latter, white shrimp. This distributional pattern furthermore reflects what has since been noted in studies of oceanic currents over the shelf of the northwestern Gulf, namely, that during spring the net nearshore drift is to the west then gradually reverses so that by midsummer it is to the east (U.S. Fish and Wildlife Service, 1963 and 1964). The obvious inferences to be drawn from these observations are that recently hatched brown and white shrimp utilizing the Galveston estuary as a nursery area generally originate on spawning grounds lying to the east and to the west, respectively.

In a similar manner we examined the distribution of young Penaeus - practically all postlarvae - in Galveston Entrance. This analysis (Table IV), which also assumed temporal effects to be fixed, tested the hypotheses of no differences between mean standardized counts from each of two depths, in two areas (V and VI in Fig. 1), during 12 mo. Expected variation among units of time was again statistically significant but, in contrast to results of the preceding analysis, the outstanding sources of variation were depths and the depths X months interaction. More individuals on the average at the lower depth is interpreted to mean an increasing adaptation to the benthic existence of older shrimp as the rapidly developing postlarvae approach and transit tidal passes such as Galveston Entrance. Of even greater interest was a change with time in their depth distribution, which appeared to be species-associated. During early spring (March-April), when the influx of brown shrimp postlarvae reaches its peak (Baxter, 1963), postlarval density was greatest at the 6-m depth. In early summer (June-July) when the immigration of white shrimp postlarvae is maximal, postlarvae were most abundant at the 1 1/2-m level. This observation may reflect a difference in the behavior, hence distribution, of postlarval white shrimp that makes estimation of their abundance when passing through Galveston Entrance much more difficult than in the case of brown shrimp postlarvae.

An attempt is made in Fig. 5 to portray the seasonal abundance of postlarval Penaeus as they move through Galveston Entrance. Unfortunately, our inability to separate the brown and white species resulted in the distribution of each being masked. The plotted data nevertheless tend to agree with those developed by Baxter (1963) in the years immediately following this study. Otherwise we are unable to offer an explanation - other than to point to vagaries of sampling - of why the fairly strong evidence of abundant larval and postlarval (white) shrimp offshore during the summer (Fig. 4) was not paralleled by corresponding evidence of postlarval abundance in Galveston Entrance (Fig. 5).

4.2 Distribution by developmental stage

Of more than passing interest in the search for answers to where, when, and how intensively the shrimps of commercial importance spawn is knowledge of the distribution of their early life history stages. It follows that delineating concentrations of the very young and transitory naupliar, protozoal, and mysis stages is tantamount to locating the parent shrimps' spawning grounds. To facilitate their examination for this

TABLE III

Analysis of variance of transformed Penaeus counts from the Gulf of Mexico off Galveston, Texas, March 1959 - March 1960.
Basic data are total prejuvenile Penaeus per 100 m³ in 10 samples each at two depths, at four distances (tiers) and in four areal sectors established radially from Galveston Entrance, and during four seasons.

Source of variation	D.f.	Sum of squares	Mean square
Seasons	3	600.73	200.24**
Sectors	3	27.67	9.22
Tiers	3	27.32	9.11
Depths	1	12.49	12.49
Sectors x Tiers	9	53.54	5.95
Sectors x Depths	3	26.17	8.72
Tiers x Depths	3	27.74	9.25
Sectors x Tiers x Depths	9	26.68	2.96
Error	77	853.53	11.08
Seasons x Sectors	(9)	(257.67)	(28.63)**
Seasons x Tiers	(9)	(191.07)	(21.23)
Seasons x Depths	(3)	(48.17)	(16.06)
Residual	(56)	(356.62)	(6.37)
Total	111	1,655.87	

** Significant at 1 percent level

TABLE IV

Analysis of variance of transformed Penaeus counts from Galveston Entrance, Texas, March 1959 - March 1960.
Basic data are average numbers of prejuvenile Penaeus per 100 m³ in 1,476 samples collected systematically as shown in Table I.

Source of variation	D.f.	Sum of squares	Mean square
Months	11	97.49	8.86**
Subareas/Months	12	10.75	0.89
Depths	1	3.93	3.93*
Depths x Months	11	34.88	3.17**
Depths x Months/Subareas	12	5.23	0.44
Total	47	152.28	

** Significant at 1 percent level

* Significant at 5 percent level

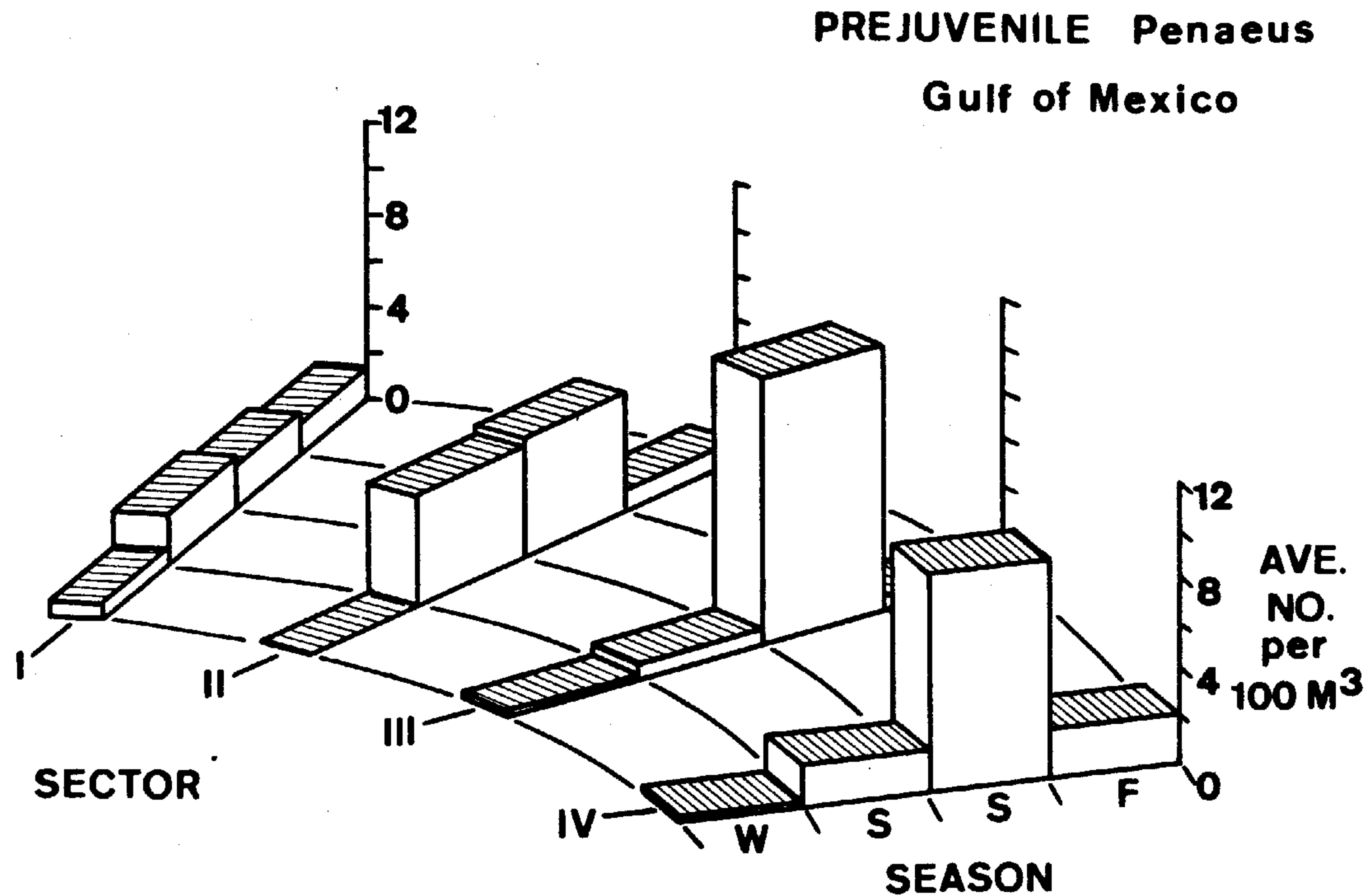


Fig. 4 The distribution of prejuvenile *Penaeus* by season and areal sector in the Gulf of Mexico off Galveston, Texas, March 1959 - March 1960.

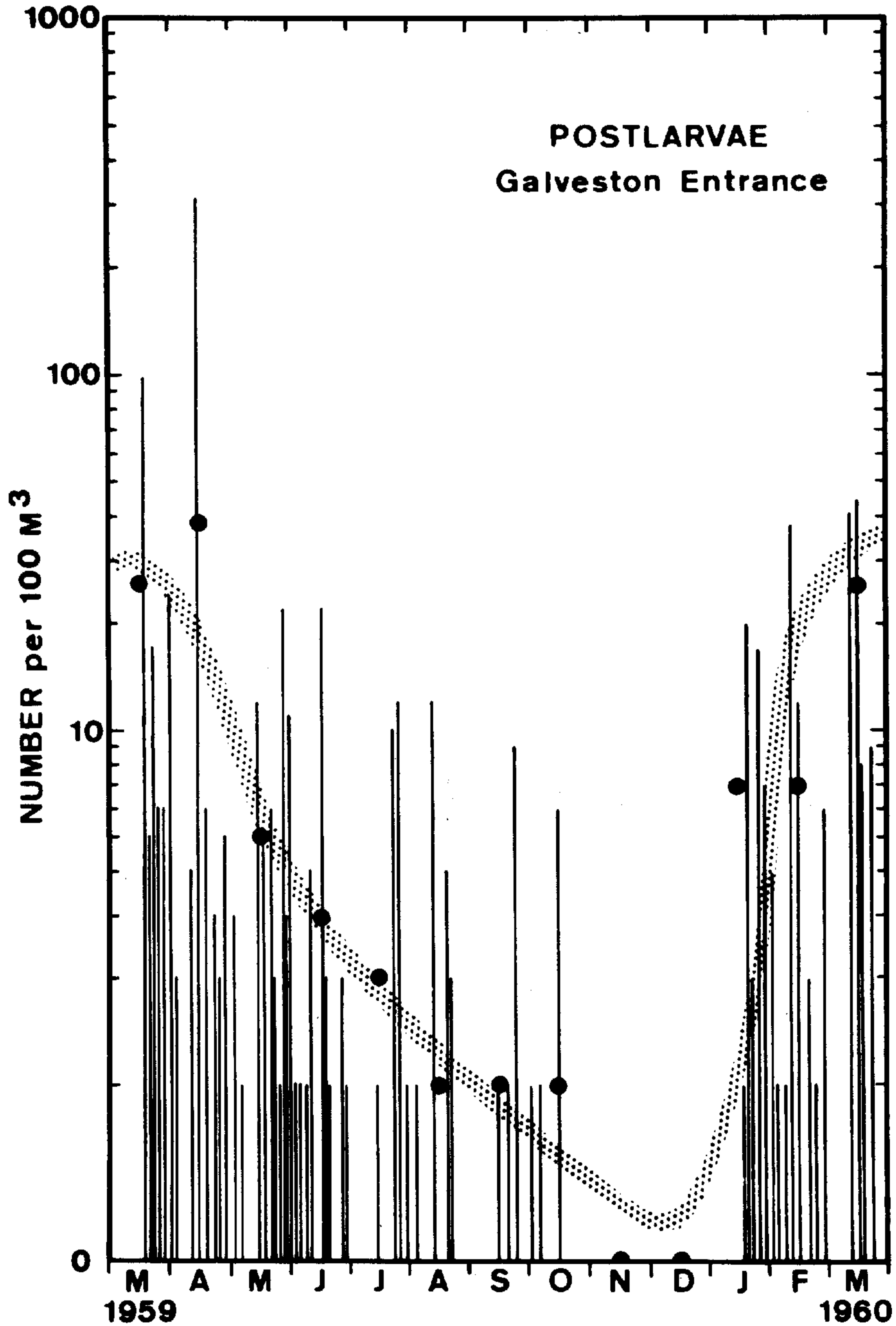


Fig. 5 Average density of postlarval Penaeus in Galveston Entrance, Texas, March 1959 - March 1960. [Shaded circles represent monthly mean numbers per 100 m³.]

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purpose we reduced the pertinent study data to mean standardized counts of each developmental stage according to season, distance from shore, and depth (Table V). Major features of the resulting tabulation are: (1) the paucity of larvae (nauplii, protozoae, and mysids) during the autumn and winter; (2) the absence of larvae at the bottom in all seasons; (3) the absence of larvae in the upper layer and in waters closer than 10 km from shore during spring when peak shoreward movement of brown shrimp larvae is expected; (4) the relatively great abundance of all stages at mid-depths and all distances from shore during the summer; and (5) the comparatively lower numbers of postlarvae on the bottom during most of the year.

Particularly interesting, in view of a prevalent theory postulating mass overwintering of brown shrimp postlarvae in nearshore waters (Kutkuhn, 1962; Temple and Fischer, 1968; and Aldrich, Wood and Baxter, 1968), was the complete absence of Penaeus postlarvae in our (52) bottom samples throughout the winter. One might question here the possibility that differential efficiency of the gear used to sample on the bottom biased our results, but re-examination of the raw data showed that early and late postlarvae of related penaeids entered bottom collections just as frequently in the winter as they did in other seasons when Penaeus postlarvae were commonly encountered at the bottom. On 8 and 22 December 1959, for example, four and five bottom (8 to 16 m) samples, respectively, yielded an average of two Xiphopenaeus krøyeri postlarvae per 100 m³; on 20 January 1960, four bottom samples contained an average of 10 Trachypenaeus spp. postlarvae per 100 m³. These observations lead us to discount gear selectivity as a possible source of data bias, and simply add to the confusion arising from speculation about the fate of young brown shrimp that hatch in the autumn but do not appear in estuaries in expected numbers during autumn and winter.

We believe it safe to say, as in the preceding analysis, that these observations largely mirror events involving two different species. The spring counts most likely represented brown shrimp that originated on spawning grounds well beyond the seaward boundary of the study area, whereas the summer counts largely represented white shrimp whose spawning grounds were situated much closer to and possibly overlapped the study area. If one accepts this view as a cogent one, the distributional patterns manifested by the data in Table V become self-explanatory.

Examination of comparably treated data from the Entrance collections (Table VI) confirms in large measure what was suggested by the data in Table V, namely, the absence of larvae in nearshore waters (0-10 km) during the autumn, winter and spring; the tendency for postlarval density to be greatest at mid-depth during the late winter and spring when the influx of young brown shrimp is maximal; and, because of the occurrence of larvae close to shore and in the tidal pass during the summer, the spawning of white shrimp not too far offshore.

4.3 Distribution according to time of day

With a single exception, all sampling throughout the study area was performed in daylight, on the assumption that diel changes in the vertical displacement of pre-juvenile Penaeus, if they occurred, remained essentially the same from sampling date to sampling date. The exception occurred in late May, within a 24-h interval during which large numbers of (white?) shrimp postlarvae passed through Galveston Entrance. In that period and location we made two identical sampling runs, both on flood tide, one in bright daylight between 0900 and 1100 CST, the other in darkness 17 h later between 0400 and 0600 CST (Table VII). Unfortunately, we did not repeat this exercise and therefore make no claim as to the conclusiveness of the data. But their analysis did allay some fear that our sampling was possibly not as efficient as it should have been because it routinely took place during that part of the day when many believed the upper 6 to 8 m of water is generally devoid of the organisms whose density we were attempting to measure. Even more convincing was a comparison of data obtained in the Gulf on 166 sampling dates when collections were taken simultaneously at three depths - 1½ m, 6 m, and on the bottom (Table VIII). We believe these data dispel any serious doubt that failure to sample in darkness as well as in daylight, i.e., to consider light intensity

TABLE V

Distribution of prejuvenile Penaeus in the Gulf of Mexico off Galveston, Texas, March 1959 - March 1960.
[Data are coded average numbers of organisms per 100 m³.]

Season	Distance from shore	Distribution of samples			Developmental stage and depth of collections											
					Nauplii**		Protozoaeae		Myses		Postlarvae					
		1 1/2 m	6 m	Bottom*	1 1/2 m	6 m	1 1/2 m	6 m	1 1/2 m	6 m	1 1/2 m	6 m	Bottom	1 1/2 m	6 m	Bottom
	Km	Number			Number x 10											
Winter	0-10	90	90	36	0	0	0	0	0	0	2	4	0			
	10-20	27	27	0	0	0	0	0	0	0	2	1	-			
	20-40	27	27	16	0	0	0	0	0	0	0	0	0			
Spring	0-10	90	90	21	0	0	0	0	0	0	21	32	93			
	10-20	25	25	3	0	0	0	12	0	7	0	10	0			
	20-40	27	27	13	0	0	0	4	0	4	10	64	0			
Summer	0-10	100	100	10	3	39	0	0	1	0	33	25	6			
	10-20	30	30	3	0	10	21	4	7	3	36	63	0			
	20-40	30	30	3	0	43	0	34	66	16	74	48	0			
Autumn	0-10	110	110	39	0	0	0	0	0	0	22	7	3			
	10-20	33	33	1	0	2	0	0	0	0	15	16	0			
	<u>20-40</u>	<u>33</u>	<u>33</u>	<u>21</u>	<u>0</u>	<u>0</u>	<u>0</u>	<u>0</u>	<u>0</u>	<u>0</u>	<u>0</u>	<u>0</u>	<u>0</u>			
Combined	0-40	622	622	166	1	9	1	2	4	1	19	20	13			

* Depth 7 to 12 m at the 12 stations within 10 km of shore
 " 15 m " " 2 " " 20 km " "
 " 15 to 16 m " " 2 " " 40 km " "

** Provisional identification

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TABLE VI

Distribution of prejuvenile Penaeus in Galveston Entrance, Texas, March 1959
- March 1960. [Data are coded average numbers of organisms per 100 m³.]

Season	Distribution of samples			Developmental stage and depth of collections					
				Protozoecae and mysids			Postlarvae		
	1 1/2 m	6 m	Bottom	1 1/2 m	6 m	Bottom	1 1/2 m	6 m	Bottom
	<u>Number</u>			<u>Number x 10</u>					
Winter	148	148	25	0	0	0	37	44	18
Spring	236	266	55	0	0	0	110	314	34
Summer	192	198	16	0	<1	0	27	16	45
Autumn	<u>144</u>	<u>144</u>	<u>22</u>	<u>0</u>	<u>0</u>	<u>0</u>	<u>9</u>	<u>6</u>	<u>13</u>
Combined	720	756	118	0	<1	0	53	124	28

TABLE VII

Comparison by depth and time of day of average numbers of Penaeus postlarvae collected in Galveston Entrance, Texas, 25-26 May, 1960. [Number of collections in parentheses]

Sampling condition	Depth			Combined
	1 1/2 m	6 m	Bottom*	
Daylight (0900-1100)	12 (8)	31 (8)	0 (4)	17 (20)
Darkness (0400-0600)	4 (8)	1 (8)	12 (4)	5 (20)
Combined	8(16)	16(16)	6 (8)	11 (40)

* Depth 7 1/2 to 10 m

as a variable significantly influencing vertical distribution of planktonic-stage Penaeus, materially biased the study's results; sampling concurrently at 1½ and 6 m was evidently enough to account for variation due to diel differences in depth distribution. Possible bias due to differential catchability of the two types of gear was also considered negligible, the rationale being that the No. 1 mesh over the codend of the trawl was small enough (420 µ) to retain the smallest larva we expected to encounter. Although Temple and Fischer (1965) demonstrated changes with time of day in the stratification of planktonic penaeids, their data are not directly comparable to ours because they combined representatives of three other genera with those of Penaeus.

More recent work still leaves unsettled, however, the question of diel changes in the distribution of postlarval Penaeus entering Galveston Bay. Whereas standardized sampling every 2 h for 4 days in Galveston Entrance (April 1963) yielded, on the average, almost twice as many postlarval brown shrimp during darkness as in daylight (U.S. Fish and Wildlife Service, 1964), a similar study in Rollover Pass (March and April 1965) indicated no relation between sampling success and time of day (U.S. Fish and Wildlife Service, 1966).

4.4 Role of environmental factors

Graphical comparison failed to reveal any apparent relation between the distributions of prejuvenile Penaeus and those of temperature or salinity. Average subsurface (3 m) temperatures closely paralleled corresponding Entrance temperatures (Fig. 6) and the only inference we feel justified in drawing at this time is that generally low winter temperatures effectively slowed postlarval movement into and through Galveston Entrance (see Fig. 5 and 6). Otherwise the data suggest nothing more than that salinity in the Entrance did not materially influence the movement of postlarvae into the bay.

TABLE VIII

Distribution of Penaeus larvae and postlarvae at three depths in the Gulf of Mexico off Galveston, Texas, March 1959 - March 1960. /Data are total numbers or organisms per 100 m³ in 498 samples, one collected simultaneously at each depth during 166 samplings. These samplings were about evenly spread over the study year and all took place in daylight. Average depth at all stations in the study area was 14 m; maximum depth at any station was 17 m./

Developmental stage	Depth		
	1½ m	6 m	Bottom
	<u>Number</u>		
Larvae*	63	270	0
Postlarvae	<u>234</u>	<u>197</u>	<u>213</u>
All	297	467	213

* Includes nauplii, protozoaeae, and mysces

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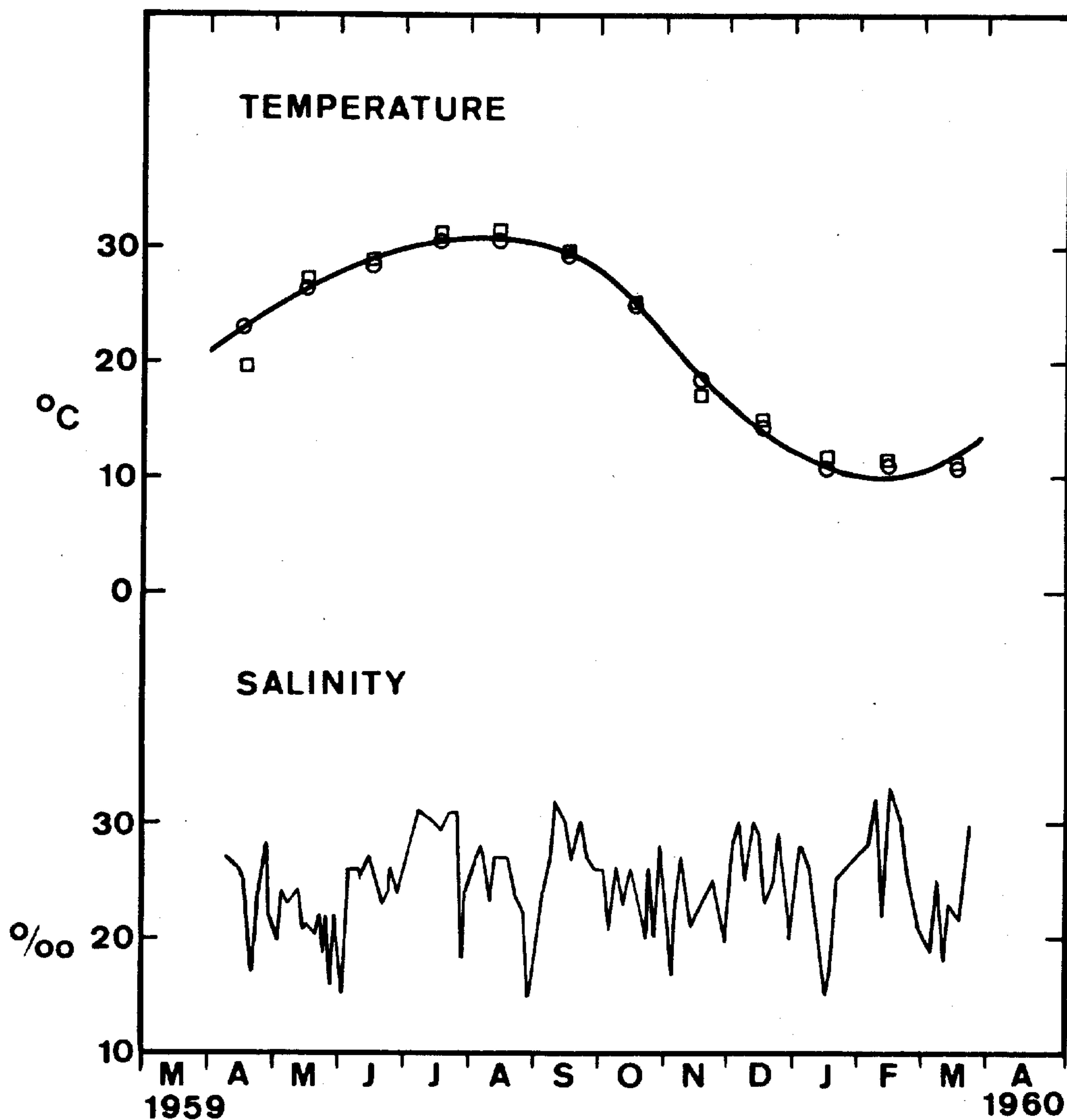


Fig. 6 Monthly average water temperature in Galveston Entrance, Texas (O), and the nearby Gulf of Mexico (□), and salinity in Galveston Entrance, March 1959 - March 1960.

5 COMPUTATION OF DENSITY

Point estimation of the overall abundance of prejuvenile Penaeus as a possible indication of spawning success was not a major objective of this study. Understandably, it would have been meaningless to present such estimates without comparative data from previous years, or good prospects for their continued acquisition in the future. But we had designed the sampling scheme with the additional purpose of density estimation in mind, and feel its statistical appraisal in this light is appropriate here.

Evaluation involved an analysis-of-variance model developed for the treatment of data collected by multistage, or nested, sampling techniques such as the one we employed (Anderson and Bancroft, 1952, p. 325). To simplify computations we selected those sets of data - each set representing a sampling day - that contained the least number of missing entries and in which the number of concentrate aliquots was uniformly two. In addition to counts of prejuvenile Penaeus, we also included in this analysis the standardized counts of all other penaeid larvae and postlarvae (Sicyonia, Trachypenaeus, and Xiphopenaeus) entering the aliquots. The sources of variation treated in our appraisal of the offshore sampling scheme were: collection dates (4), radiating transects (4), stations along each transect (4), depths at each station (2), and aliquots (sub-samples) from the single collection at each depth (2). In the Entrance survey, the sources were: collection dates (8), subareas (2), stations in each subarea (4), depths at each station (2), and aliquots from the single collection at each depth (2). In both offshore and inshore surveys the number of sampling dates constituted a small fraction of all possible dates and, accordingly, the sampling rates in the remaining subclasses were small. Because the analysis entailed no probability statements, transformation of the Poisson aliquot counts (number per 10 m³) was unnecessary.

The resulting analysis for the offshore sampling scheme (Table IXA) disclosed that, aside from the large expected variability among dates, the major source of variation was between depths. Without increasing the overall sampling rate, survey efficiency could have been improved 15 percent by doubling the number of transects and halving the number of stations on each, and an additional 7 percent by also doubling the number of depths and halving the number of aliquots (Table IXB). Similarly, the sampling rate could have been reduced a significant 25 percent with a loss in efficiency of only 3 percent had the number of stations been reduced to two per transect, the number of depths (or samples) at each station increased to six, and the number of aliquots reduced to one.

The corresponding analysis for the study's inshore survey identified areas, stations, and depths (apart from dates) as roughly equivalent sources of variation (Table X). Computation of predicted variances for different combinations of survey variables, showed that no change in the initial procedure would have led to more efficient sampling, or to a reduced sampling rate with the same level of efficiency. Hence the reduction in stations in subarea V from four to two early in the study did contribute to a slight decrease in sampling efficiency.

In the assessment of both offshore and inshore surveys, variation between aliquots proved negligible. Thus, counts from a single aliquot would have sufficed during routine examination of sample concentrates. Actually, only 4 percent of the 3,004 samples examined during the study were so treated; 60 percent were processed by making counts in two aliquots and the remaining 36 percent by examining the entire concentrate.

The foregoing analyses demonstrate the high degree of variability with time in the density of prejuvenile penaeids. The relatively high coefficients of variation associated with the estimated mean numbers of larvae and postlarvae per unit volume (Tables IXA and X) could have been reduced significantly only by more frequent sampling. We believe that while control of spatial variation is essential in surveying for the abundance of prejuvenile Penaeus, future work should consider more frequent sampling than was scheduled in this study if the reliability of density estimates is to be increased to more acceptable levels.

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TABLE IX

Appraisal of scheme to sample for density of prejuvenile penaeids in Gulf of Mexico off Galveston, Texas, March 1959 - March 1960.
A: Analysis of variance of selected sampling data (number of organisms per 10 m³). B: Percent increase in sampling efficiency based on predicted variances of mean density using indicated combinations of sampling variables.

A

Source of variation	D.f.	Sum of squares	Mean square	Estimated variance component
Dates	3	289.23	96.41	$s_{Dt}^2 = 0.70$
Transects/Dates	12	616.55	51.38	$s_T^2 = 1.76$
Stations/Transects	48	1,115.56	23.24	$s_{St}^2 = 1.85$
Depths/Stations	64	1,015.25	15.86	$s_D^2 = 7.03$
Subsamples/Depths	<u>128</u>	<u>231.50</u>	1.81	$s_{SS}^2 = 1.81$
Total	255	3,268.09		
$\bar{X} = 1.68 / 10 \text{ m}^3$ $s^2(\bar{X}) = \frac{s_{Dt}^2}{4} + \frac{s_T^2}{16} + \frac{s_{St}^2}{64} + \frac{s_D^2}{128} + \frac{s_{SS}^2}{256} = 0.38$ <p>Coef. Var. (\bar{X}) = 0.36</p>				

B

Stations		2			4			8		
Depths		2	4	6	2	4	6	2	4	6
Transects	Subsamples									
2	1	-109	-72	-60	-57	-38	-32	-31	-22	-19
	2	-101	-68	-58	-53	-37	-31	-29	-21	-18
	3	-99	-67	-56	-52	-36	-31	-28	-20	-18
	All	-94	-65	-55	-49	-35	-30	-27	-20	-18
4	1	-28	-9	-3	-2	7	10	11	16	17
	2	-24	-7	-2	0	8	11	12	16	18
	3	-23	-7	-2	1	9	11	12	16	18
	All	-20	-6	-1	2	9	12	13	17	18
8	1	13	22	25	26	30	32	32	34	35
	2	15	23	26	27	31	32	33	35	36
	3	15	23	26	27	31	32	33	35	36
	All	16	24	26	28	31	33	33	35	36

TABLE X

Appraisal of scheme to sample for density of prejuvenile penaeids in Galveston Entrance, Texas, March 1959 - March 1960: Analysis of variance of selected sampling data (number of organisms per 10 m³).

Source of variation	D.f.	Sum of squares	Mean square	Estimated variance component
Dates	7	117.94	16.85	$s_{Dt}^2 = 0.39$
Subareas/Dates	8	33.75	4.22	$s_{SA}^2 = 0.05$
Stations/Subareas	48	163.00	3.40	$s_{St}^2 = 0.04$
Depths/Stations	64	227.75	3.56	$s_D^2 = 1.29$
Subsamples/Depths	<u>128</u>	<u>126.00</u>	0.98	$s_{SS}^2 = 0.98$
Total	255	668.44		
$\bar{X} = 0.83 / 10 \text{ m}^3$ $s_{(\bar{X})}^2 = \frac{s_{Dt}^2}{8} + \frac{s_{SA}^2}{16} + \frac{s_{St}^2}{64} + \frac{s_D^2}{128} + \frac{s_{SS}^2}{256} = 0.07$ <p>Coef. Var. (\bar{X}) = 0.31</p>				

6 SUMMARY

In early 1959 the Bureau of Commercial Fisheries began a study to determine when, from what direction, at what stage of development, how many, and under what conditions, prejuvenile shrimp of the economically important genus Penaeus enter the extensive Galveston (Texas) estuary. The study's findings, together with the results of subsequent work, were to aid in circumscribing offshore spawning areas and provide information on the extent to which the progeny of shrimp reproducing in each area are nurtured in each estuary bordering the northern Gulf of Mexico.

The study area consisted of two subdivisions, the Entrance itself and about 1,500 km² of the adjoining Gulf. Sampling for the planktonic-stage Penaeus proceeded synoptically in both areas with Gulf-V plankton nets and intermittently with a small trawl. The sampling scheme permitted assessment of variations in the young shrimps' horizontal, vertical, and temporal distribution. Limited resources precluded control of variation due to such factors as time of day, stage of tide, and quality of environment.

Over 3,000 collections obtained during 53 wk of sampling - one biological year - yielded the data on which the study was based. The more significant results of their analysis may be summarized as follows:

(1) Despite a comparatively high sampling frequency, once every 9 days in the nearby Gulf and once every 3 days in Galveston Entrance, the temporal distribution of collections was insufficient to trace the fairly rapid movement of newly hatched broods of shrimp from offshore spawning grounds into the important Galveston Bay nursery area.

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(2) The data revealed, however, that horizontal distribution of Penaeus larvae and postlarvae in the Gulf, and vertical distribution of Penaeus postlarvae in the Entrance, changed markedly with the seasons. During the summer, most prejuvenile Penaeus approached the Entrance from the south and west, whereas in the late winter and early spring, most young shrimp moved in from the east. Postlarvae moving through the Entrance in summer distributed themselves more uniformly in the water column than did those passing through in spring when greater numbers were encountered in the lower strata.

(3) Except during the summer few Penaeus larvae entered collections within 10 km of shore. Identifying each species on the basis of its expected spawning time (re Item (2) above), we further inferred that white shrimp generally spawn in shallower water than do brown shrimp.

(4) Failure of the sampling scheme to account for possibly significant variation in the distribution of prejuvenile shrimp with time of day did not seriously bias the study's findings.

(5) Penaeus larvae were never detected in collections from the bottom; rarely did postlarvae occur in greater abundance at the bottom than at higher levels of the water column; and not once during the winter were postlarvae observed on the bottom at off-shore stations.

(6) The data provided no evidence of a functional relationship between corresponding distributions of prejuvenile Penaeus and of environmental factors (specifically temperature and salinity).

(7) For estimating density of prejuvenile penaeids, the sampling scheme employed in this study was relatively inefficient to the degree that it failed to account for wide temporal variation in organism abundance. On the other hand, it incorporated adequate control of spatial variation, although slight changes in the distribution of sampling effort would have led to more reliable density estimates.

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